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Spatial association between cod and capelin: a perspective on the inshore-offshore dichotomy

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Abstract

Northern cod (*Gadus morhua*) and capelin (*Mallotus villosus*), their major prey, have both exhibited major changes in spatial distribution during the 1990s. To study the influence of these changes on the predator-prey interaction between cod and capelin, we computed numbers of potential capelin prey surrounding cod predators (potential contact) from spring acoustic survey data. Between 1989 and 1994 the distribution of cod NAFO 2J3KL shifted to the south and east. This distribution shift occurred at the same time as similar changes in capelin spatial distribution, and potential contact between cod and capelin did not decrease in spring surveys from 1991-1994. Since the mid-1990s cod have been concentrated inshore with low densities offshore. Potential contact of remaining cod with capelin is high. High acoustic densities of capelin were observed inshore in spring 1998 and 1999 in Placentia Bay and Trinity Bay close to aggregations of cod. Offshore, acoustic estimates of capelin density and biomass in 1998 and 1999 were low compared to the 1980s. We suggest that cod are unlikely to re-establish offshore areas in 2J3KL unless capelin abundance offshore increases. There have been encouraging signs of a return to a more northerly distribution of capelin off southern Labrador in 1998 and 1999, and we are currently monitoring the response of northern cod to this change.

Résumé

L'aire de répartition de la morue du Nord *(Gadus morhua)* et celle du capelan *(Mallotus villosus)*, sa principale proie, ont subi des modifications importantes au cours des années 1990. Afin d'étudier l'effet de ces changements sur l'interaction prédateur-proie, nous avons calculé le nombre de capelans pouvant se trouver à proximité des morues prédatrices (possibilité de rencontre) à partir des données des relevés acoustiques de printemps. L'aire de répartition de la morue des divisions 2J3KL de l'OPANO s'est déplacée vers le sud et l'est entre 1989 et 1994. Ce déplacement est survenu simultanément à des changements similaires de distribution spatiale du capelan, et la possibilité de rencontre entre morue et capelan n'a pas diminuée lors de relevés de printemps de 1991 à 1994. Depuis le milieu des années 1990, les morues se sont concentrées en zone côtière, les densités étant faibles au large. La possibilité de rencontre des morues restantes avec les capelans demeure élevée. De fortes densités acoustiques de capelan ont été notées en zone côtière au printemps de 1998 et de 1999 dans la Placentia Bay et la Trinity Bay, à proximité des concentrations de morue. Au large, les estimations acoustiques de la densité et de la biomasse du capelan obtenues en 1998 et 1999 étaient faibles comparativement à celles obtenues au cours des années 1980. Nous formulons l'hypothèse qu'il est peu probable que la morue se rétablisse dans la zone hauturière de 2J3KL à moins que l'abondance du capelan n'y augmente. Des indices prometteurs d'un retour à une répartition plus nordique du capelan au large de la partie sud du Labrador ont été notés en 1998 et 1999 et nous surveillons actuellement la réaction de la morue du Nord à ce changement.

Introduction

Capelin (*Mallotus villosus*) is a major prey of cod (*Gadus morhua*) in Newfoundland waters (review by Lilly 1987). Despite their importance as prey, relatively little is known about the influence of capelin on cod spatial distribution. Historically, the inshore movement of northern cod in spring (Rose 1993) coincided with the inshore spawning migration of capelin (Akenhead et al. 1982), and it was suggested that cod "follow" the movements of capelin at this time (Templeman 1965).

During the early 1990s the spatial distribution of capelin in NAFO 2J3KL changed dramatically (review by Carscadden & Nakashima 1997). Acoustic surveys, bottom-trawl surveys and cod-stomach-content analysis all showed a shift in the distribution of capelin towards the south and east. This is illustrated by comparing capelin catches from the fall (October-December) bottom-trawl survey in 1989 and 1994 (Fig. 1). Capelin virtually disappeared from the northern part of their range, and the centre of the concentration of maturing fish shifted from NAFO 2J to southern 3K and 3L (Carscadden & Nakashima 1997). At the same time capelin increased in areas such as the Flemish Cap and Scotian Shelf where they were not common previously (Frank et al. 1996).

The spatial distribution of cod also shifted to the south and east in the early 1990s (Rose et al. 2000) in the same way as the distribution of capelin. Several authors (deYoung & Rose 1993, Lilly 1994, Rose et al. 2000) have suggested a link between spatial distributions of cod and capelin during this period, but few quantitative studies have been published.

Since the mid-1990s there has been a marked contrast in the abundance of 2J3KL cod between inshore and offshore (Lilly et al. 1999). Cod densities have remained very low offshore, but concentrations of cod are observed inshore, particularly in Smith Sound, Trinity Bay. There has been no consideration of the possible influence of capelin during this period.

In this paper, we explore the influences of changes in the geographic distribution of cod and capelin in the 1990s on the potential for capelin predation by cod. Our objective is to present a "cod's-eye view" of the distribution and abundance of capelin off Newfoundland from acoustic surveys conducted during spring 1991-1994 and in 1998 and 1999. We compare the results of inshore and offshore surveys and discuss the implications of the current distribution of capelin for cod stock recovery.

Methods

Acoustic Data

Acoustic data on cod and capelin distributions were collected during spring research surveys in 1991-1994 and in 1998 and 1999 (Table 1). Surveys in May-July 1991-1994 mapped cod and capelin distributions on the northeast Newfoundland Shelf (NAFO 3KL)

using a Biosonics 102 dual-beam 38-kHz echo-sounder calibrated with a tungsten carbide standard target. Surveys in June 1998 and June 1999 covered Smith Sound and the outer part of Trinity Bay (3L), Placentia Bay (3Ps), and the Hawke Channel area of southern Labrador (2J) using a similarly calibrated Simrad EK500 split-beam 38-kHz echo-sounder. Another survey directed at capelin in May 1999 covered the offshore part of 3KL with the same calibrated EK500 echo-sounder.

Signals from cod and capelin were distinguished based on signal characteristics and information from targeted fishing sets made using IYGPT mid-water and Campelen bottom trawls. Acoustic data were integrated in 100m horizontal bins and scaled by target strength (TS) to give estimates of areal density (fish m^{-2}) of cod and capelin in each 100m bin. Mean target strengths were calculated from fishing set length-frequency data using the relationship $TS = 20\log L - 66$ (Rose & Porter 1996) in 1991-1994 or $TS = 20\log L - 67.5$ (Rose unpublished data) in 1998-1999 for cod, and $TS = 20\log L - 73.1$ for capelin (Rose 1998) where L is fish total length in cm. Areal density estimates were grouped into larger bins corresponding to 0.05° of latitude by 0.05° of longitude (equivalent to ~5.6km by ~3.7km at 49° N) prior to statistical analysis to reduce computational time and to compensate for differences in sampling intensity between areas.

Two further surveys were conducted in the fall (August-September) of 1998 and 1999 to estimate capelin abundance in NAFO 2J3K. Acoustic measurements were made as part of the Pelagic Juvenile Survey with the same calibrated 38-kHz EK500 split-beam echo-sounder used in spring acoustic surveys. Signal identified as capelin was integrated and scaled using a TS of –34dB kg^{-1} (cf. Miller & Lilly 1991) to allow direct comparison with results from Canadian fall acoustic surveys conducted in the 1980s and early 1990s (Miller & Lilly 1991, Miller 1995). Details of these surveys, acoustic methods and statistical estimation of biomass is provided by O'Driscoll et al. (2000).

Statistical Analysis

Potential contact (O'Driscoll et al. submitted, O'Driscoll & Rose in press) is a measure of the average number of potential capelin prey within a given radius of any cod. The potential contact between cod and capelin at cod ambit radius t is given by:

$$PC(t) = \pi t^2 E[b(t)] \qquad (1)$$

Where $E[b(t)]$ is the expected density of capelin within distance t of any cod. $E[b(t)]$ may be estimated from acoustic estimates of cod and capelin density by the expressions:

$$E[b(t)] = \frac{\sum_{i=1}^{n} a_i (\overline{b_{ij}})}{\sum_{i=1}^{n} a_i} \qquad (2)$$

and $$\overline{(b_{ij})} = \frac{\sum_{j=1}^{n} (I_{ij}) b_j}{\sum_{j=1}^{n} I_{ij}} \qquad (3)$$

$E[b(t)]$ is calculated empirically as a weighted average. For each sample point i = 1,2, ...n, capelin density estimates (b_j) from all points j within distance t (indicator function I_{ij} = 1 where distance $ij < t$, 0 otherwise) are averaged, and scaled by the density of cod at point i (a_i). The result is then summed and divided by the sum of the cod density estimates to estimate the expected density of capelin within distance t. The weighted sample variance of $E[b(t)]$ may be calculated similarly by substituting s_{ij}^2 for $\overline{b_{ij}}$ in equation (2). s_{ij}^2 is the sample variance of all capelin densities ($(I_{ij})b_j$) within distance t of point i.

Results

Cod and capelin were observed in close proximity on the northeast Newfoundland Shelf in spring 1991-1994 (Fig. 2). Typically capelin were detected inshore (to the west) of cod aggregations and in shallower water, but there was extensive overlap between spatial distributions (Fig. 2), and interactions between cod and capelin were often observed (see Rose 1993 for example echogram). Potential contact between cod and capelin at cod ambits from 10-100km was high (Fig. 3a). On average there was between 85 million (1992) and 2,500 million (1993) capelin within a 40km radius of any cod (Fig. 4). The difference between years was statistically significant (one-way ANOVA $F_{3,142} = 7.25$, $p < 0.001$). Variation in potential contact (Fig. 3a) was probably related to survey timing. In 1991 and 1992 cod were still offshore in spawning aggregations during the survey. Cod spawning was earlier in 1993 and cod were observed further inshore, so potential contact with capelin was higher. In 1994 densities of cod were very low and most fish were immature.

In spring 1998 and 1999 inshore aggregations of cod were also close to concentrations of capelin. Smith Sound, Trinity Bay contains probably the largest remaining group of northern cod. This group of cod was adjacent to concentrations of capelin in outer Trinity Bay in 1998 and 1999 (Fig. 5). In June 1999 high densities of capelin were detected inside Smith Sound and cod were observed acoustically up to 100m of the bottom feeding on capelin. Potential contact between cod and capelin was very high (Fig. 3b). At an ambit radius of 40km there were 2,900 and 4,800 million capelin surrounding cod in 1998 and 1999 respectively (Fig. 4). The difference in potential contact between 1998 and 1999 was not significant ($Z = 0.997$, $p > 0.05$).

High potential contact between cod and capelin was also observed in spring surveys in Placentia Bay (Fig. 6). Capelin biomass in Placentia Bay decreased by an order of

magnitude between spring 1998 and 1999 (O'Driscoll & Rose 2000). As a consequence, potential contact with capelin was significantly lower in 1999 than in 1998 (Figs. 3c, $Z = 5.305$, $p < 0.001$). Even with the reduction in capelin biomass in 1999, contact between cod and capelin was similar to values observed on the northeast Newfoundland Shelf in the early 1990s. On average there were 400 million capelin within a 40km radius of cod in Placentia Bay in spring 1999 (Fig. 4).

Relatively few capelin were observed during an offshore survey on the northeast Shelf in spring 1999 and only one small aggregation of adult cod was detected (Fig. 7). Because there were so few cod, we did not examine contact between cod and capelin directly from this survey. The survey in 1999 covered a similar area at approximately the same time of year as acoustic surveys in 1991-1994 (Fig. 2). We superimposed the distribution of cod from surveys in the early 1990s onto the 1999 survey track and calculated potential contact between the historic distributions of cod and the observed (1999) distribution of capelin in the common area (Fig. 8). We were interested whether an offshore distribution of cod, similar to those observed from 1991-1994 would experience high contact with capelin in 1999. In all cases potential contact with capelin in 1999 would have been lower than in the early 1990s (Fig. 3d). Within a 40km cod ambit potential contact with capelin in 1999 was 25% (1991 cod distribution), 3% (1992), 14% (1993) or 46% (1994) of the level of contact measured during the original surveys (Fig. 4). Because of the relatively low sample sizes within the common survey area (Table 1), the decreases between contact measured in the original survey and contact with a 1999 capelin distribution were not statistically significant except for the 1993 cod data ($Z = 2.74$, $p = 0.006$). Potential contact between modelled offshore distributions of cod and observed capelin in 1999 was lower than potential contact with capelin measured around actual inshore cod aggregations in 1998-1999 (Fig. 4).

Capelin biomass estimated from offshore fall acoustic surveys in 2J3K in 1998 and 1999 (Fig. 9) was also low. Using a capelin *TS* of –34 dB kg^{-1} O'Driscoll et al. (2000) estimated biomass in 2J3K at 86,000 tons (95% confidence interval 36,000-135,000 tons) in 1998 and 69,000 tons (33,000-116,000 tons) in 1999. Note that these estimates do not include the inshore bays or areas of 2J3K to the north and east beyond the survey boundaries (Fig. 9). Estimates of capelin biomass in 2J3K in 1998 and 1999 were similar to estimates from equivalent Canadian fall acoustic surveys in the early 1990s and lower than all estimates from 1981-1990 (Fig. 10).

There was evidence of a northward shift in the spatial distribution of capelin in the late 1990s. In our 1998 fall survey highest densities of capelin were detected off St. Anthony, with smaller aggregations north of Fogo Island, on outer Funk Island Bank and off Cape Bonavista (Fig. 9). Capelin were concentrated further north in 1999, with peak densities off southern Labrador. Capelin were also detected on outer Funk Island Bank, on the Northeast Grand Banks and in Conception Bay in 1999 (Fig. 9).

This northward shift in capelin distribution was also evident in spring acoustic data from the Hawke Channel region of southern Labrador. Spring acoustic surveys for cod have

been conducted in Hawke Channel since 1994. Capelin were first detected on these surveys in June 1998 (Fig. 11). In June 1999 capelin abundance in the survey area had increased by two orders of magnitude and capelin were observed throughout the southeastern part of Hawke Channel (Fig. 11). Because of this northward shift in capelin distribution, potential contact between the small group of remnant cod present in Hawke Channel and capelin increased significantly between spring 1998 and 1999 (Fig. 3e, $Z = 5.556$, $p < 0.001$). However, potential contact between cod and capelin in Hawke Channel in spring 1999 was still lower than contact measured in inshore areas of Trinity Bay and Placentia Bay during the same survey (Fig. 4).

Discussion

Despite changing spatial distributions of cod and capelin during the 1990s potential contact between cod and capelin in the spring has not decreased. There is no evidence that the current inshore "pockets" of cod are limited by capelin availability. Cod in Trinity Bay and in Placentia Bay in spring 1998 and 1999 were observed close to, and feeding on, aggregations of capelin. Levels of potential contact with capelin prey inshore in the late 1990s were similar to, or greater than, potential contact from 1991-1994 offshore on the northeast Newfoundland Shelf.

Capelin abundance offshore in 1998 and 1999 was low and may be limiting the expansion and recovery of northern cod stocks. We showed that under current capelin distribution patterns (spring 1999), an offshore distribution of cod similar to that of the early 1990s would experience lower levels of contact with capelin prey than they had earlier in the decade. We suggest the implication of the current spatial distribution of capelin is that cod will be less likely to re-establish offshore 2J3KL unless capelin abundance offshore increases.

Our low estimates of capelin biomass offshore are in agreement with the public perception in Newfoundland that capelin numbers have declined in the 1990s (Nakashima & Clark 1998). However, inshore indices of capelin abundance have remained relatively unchanged during the 1980s and 1990s (e.g. Carscadden & Nakashima 1997), despite changes in spawning time and fish length (Carscadden et al. 1997). We hypothesise that the apparent discrepancy between views of the stock based on inshore and offshore estimates of abundance may be due in part to the persistence of concentrations of capelin inshore, especially in Trinity Bay where most estimates of inshore spawning abundance are carried out. The presence of inshore or "coastal" capelin is not a recent phenomenon. Winters (1969) described the presence of large over-wintering concentrations of capelin in Trinity Bay in February to April 1968. We have also observed relative high densities of capelin in the outer part of Trinity Bay during surveys in January 1999 and 2000. We do not wish to speculate on the absolute biomass of capelin inshore in 2J3K, but suggest that the *relative* importance of the inshore to capelin, as well as cod, may have increased in the 1990s with declines in offshore abundance.

The northward shift in capelin distribution of capelin we observed between 1998 and 1999 is consistent with the trend in the distribution of capelin catches from fall (October to December) bottom-trawl surveys (Lilly 2000). In 1998 and 1999 large catches of capelin were made further north than in 1995-1997 (Lilly 2000). These observations of more northerly offshore distributions of capelin in 1998 and 1999 suggest that capelin are returning to historical distribution patterns. We believe this is encouraging for cod. The "right site" hypothesis (deYoung & Rose 1993) predicts that a northern offshore distribution of cod is favourable for recruitment. The southern distribution of capelin in the early and mid 1990s would have resulted in poor feeding conditions for cod on these critical areas of the northern shelf. We are continuing to monitor the response of cod in the Hawke Channel area to the increase in capelin. We are hopeful that re-establishment of capelin in this northern region will result in increased productivity of existing cod and immigration of fish from other areas.

Our measure of potential contact is based only on the relative spatial arrangement of cod and capelin and does not imply cod encounter, or even have the ability to detect all capelin within their ambit. We assume, however, that at spatial scales similar to the foraging ambit that potential contact is a measure of feeding opportunity. This assumption is supported by evidence from studies on cod feeding. Lilly (1994) did not detect a decrease in the amount of capelin in cod stomachs from fall samples in 3KL during the early 1990s. This agrees with our observation that there was relatively high potential contact between cod and capelin on the northeast Newfoundland Shelf in spring 1991-1994. Seasonal patterns in potential contact with capelin in Placentia Bay also match observations of seasonal changes in feeding on capelin by cod (O'Driscoll & Rose in press). Finally, in samples from spring 1998 and 1999 potential contact with capelin in a 40km radius was significantly correlated with cod liver condition index (Fig. 12, Spearman's rank correlation, $n = 6$, $rho = 0.943$, $p = 0.005$). Liver condition index (liver weight * gutted weight^{-1}) is a measure of lipid storage and is considered to be a good measure of feeding on capelin (Yaragina & Marshall in press).

Work in the Barents Sea has established clear links between capelin abundance and cod stock structure (Nilssen et al. 1994, Yaragina & Marshall in press). We think it is important that the role of capelin is similarly considered in Newfoundland waters

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Table 1. Summary of spring acoustic surveys used to estimate potential contact between cod and capelin.

Year	Area	Survey timing	No. of 0.05° lat. by 0.05° long. samples	Maximum sample separation (km)	Capelin density (fish m^{-2})		Cod density (fish m^{-2})	
					Mean	Std. Dev.	Mean	Std. Dev.
1991	3KL Offshore	5/13-6/28	1039	593	0.1650	0.7420	0.0077	0.0177
1992	3KL Offshore	6/8-7/14	674	304	0.0868	1.0497	0.0172	0.0946
1993	3KL Offshore	6/6-6/28	1224	624	0.3951	0.7009	0.0027	0.0165
1994	3KL Offshore	6/13-6/27	613	541	0.1426	0.3467	0.0004	0.0018
1998	Trinity Bay	6/7-6/9	147	309	0.1656	0.6274	0.0007	0.0031
1998	Placentia Bay	6/18-6/25	288	274	1.5000	3.5418	0.0014	0.0075
1998	Hawke (2J)	6/11-6/17	311	249	0.0004	0.0041	0.0002	0.0005
1999	Trinity Bay	6/7-6/18	51	84	0.6819	1.4996	0.0008	0.0018
1999	Placentia Bay	5/31-6/4	307	274	0.1016	0.3028	0.0003	0.0007
1999	Hawke (2J)	6/11-6/15	263	305	0.0372	0.0618	0.0001	0.0004
1999	3KL Offshore	5/12-5/28	595	424	0.0836	0.4684	-	-
1999/91	3KL Overlap	-	128	366	0.0480	0.1692	0.0073	0.0164
1999/92	3KL Overlap	-	120	270	0.0427	0.1770	0.0249	0.1384
1999/93	3KL Overlap	-	110	389	0.0899	0.3874	0.0021	0.0070
1999/94	3KL Overlap	-	70	290	0.0947	0.4441	0.0005	0.0024

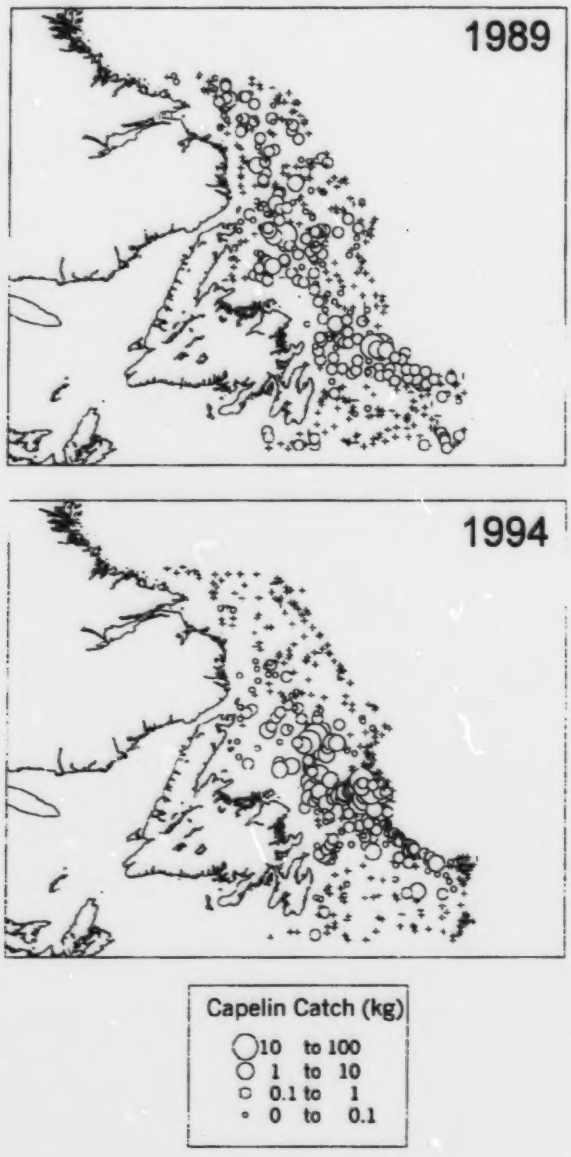

Fig. 1. Distribution of capelin catches from fall (October-December) bottom-trawl surveys in 1989 and 1994.

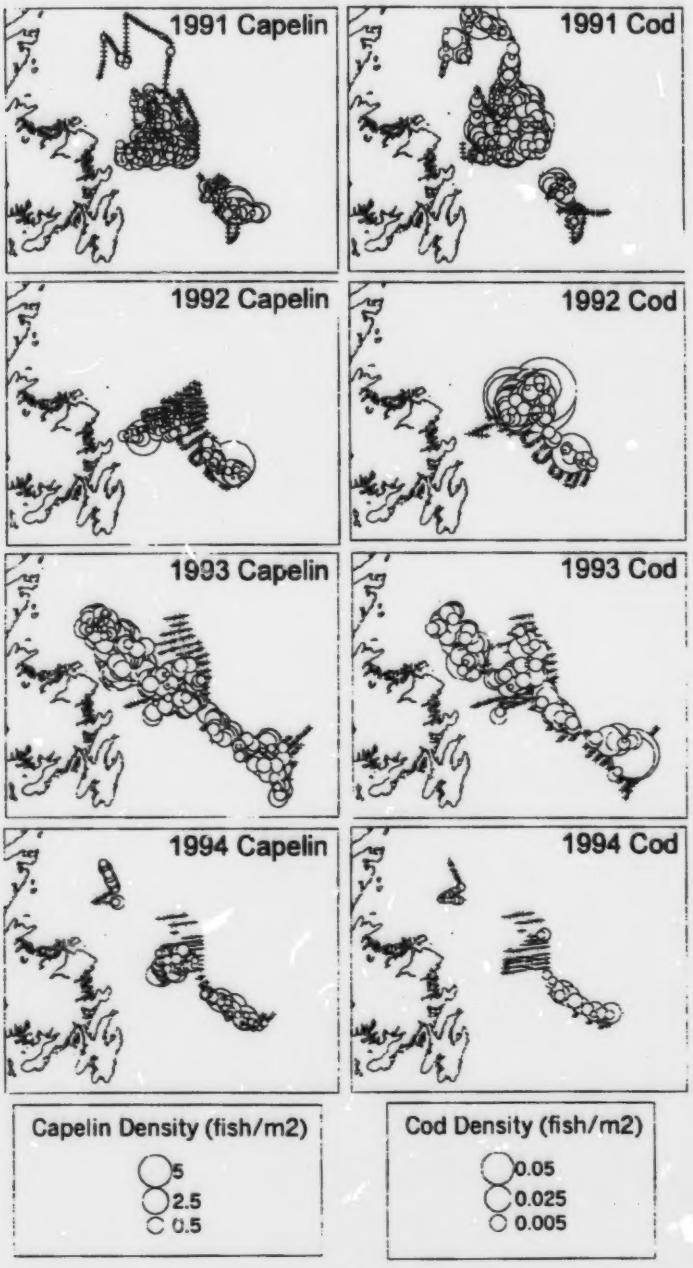

Fig. 2. Capelin and cod distributions on the Northwest Newfoundland shelf from acoustic surveys in May-June 1991-1994. '+' symbol indicates no fish were detected.

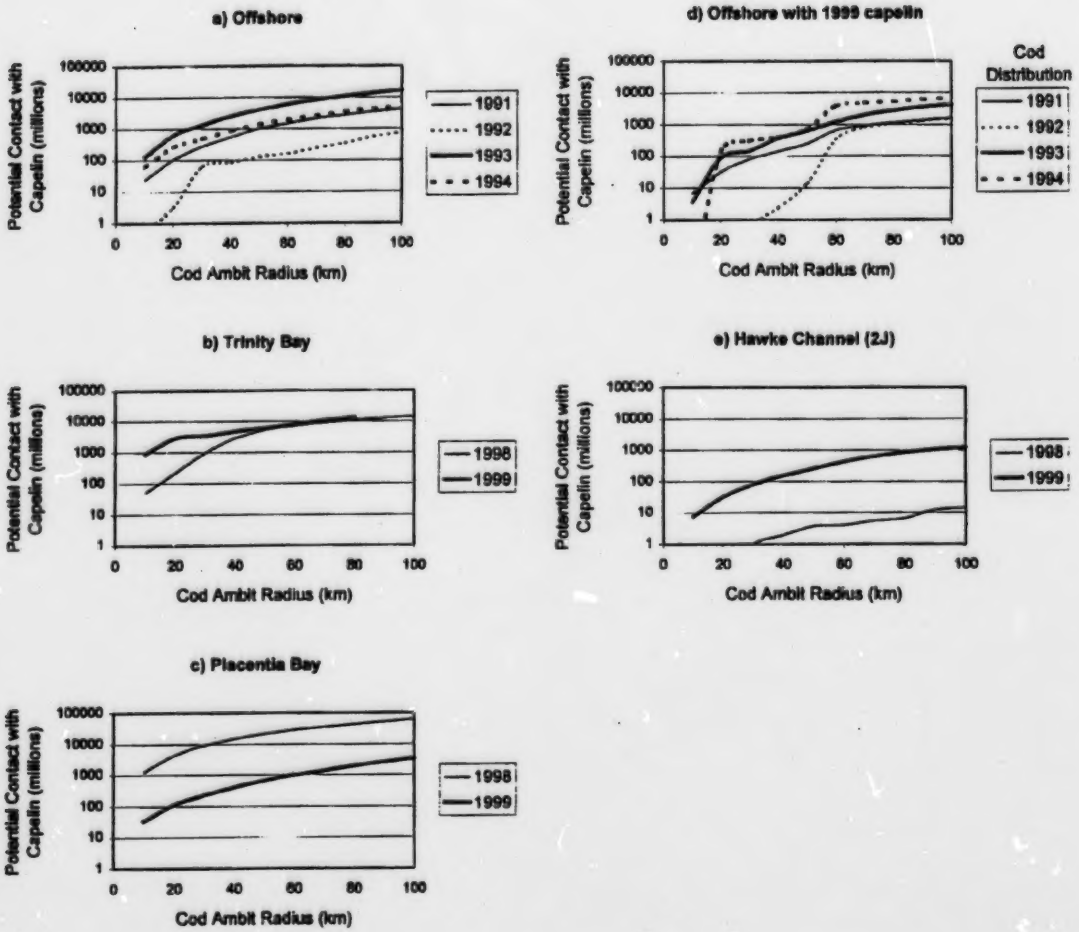

Fig. 3. Potential contact between cod and capelin over a range of possible cod ambits from spring acoustic survey data: a) northeast Newfoundland Shelf 1991-1994 (Fig. 2); b) Trinity Bay 1998-1999 (Fig. 5); c) Placentia Bay 1998-1999 (Fig. 6); d) northeast Newfoundland Shelf comparing cod distributions from early 1990s with capelin distribution from 1999 (Fig.8); e) Hawke Channel Labrador 1998-1999 (Fig. 11).

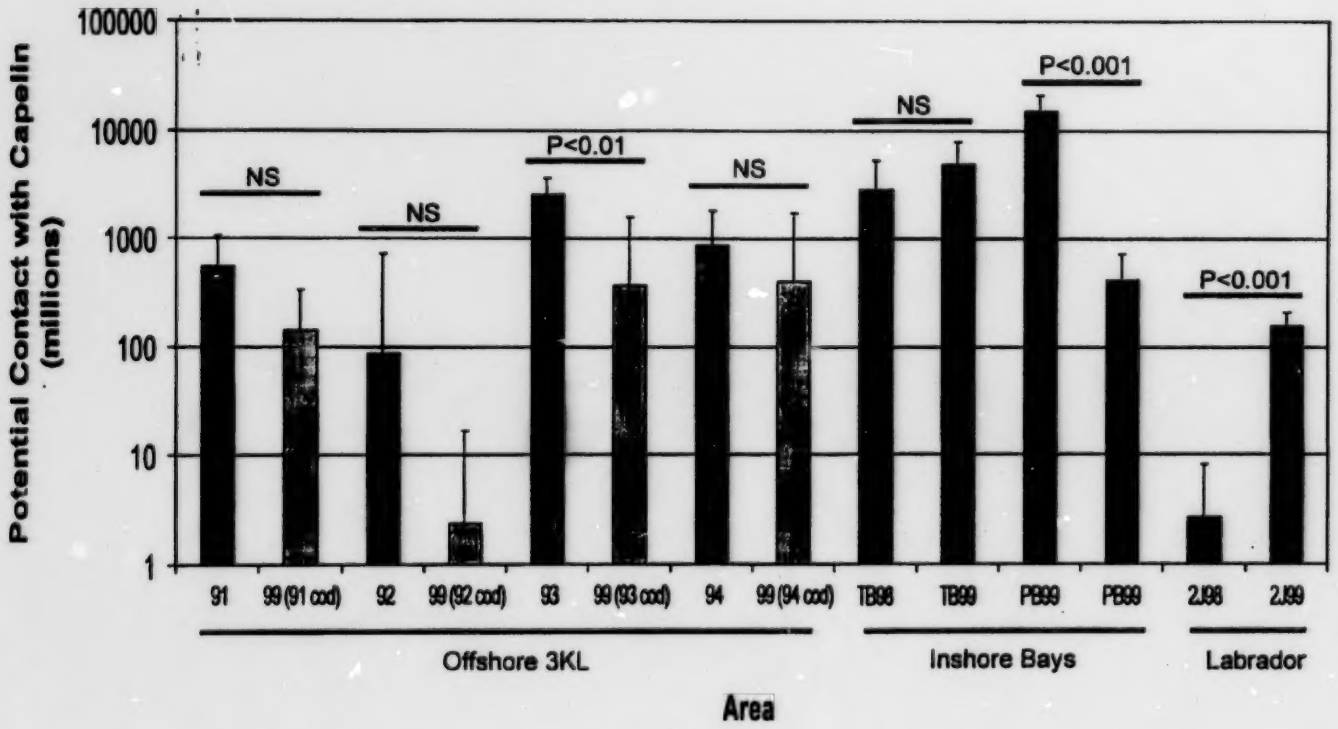

Fig. 4. Spatial and temporal differences in spring potential contact between cod and capelin in the 1990s. Bars compare potential contact at a cod ambit radius of 40km + 2 standard errors. Grey bars show contact between modelled distributions of cod and observed 1999 distribution of capelin offshore (Fig. 8). Black bars show contact between cod and capelin measured during the same acoustic survey. TB = Trinity Bay, PB = Placentia Bay, 2J = Hawke Channel.

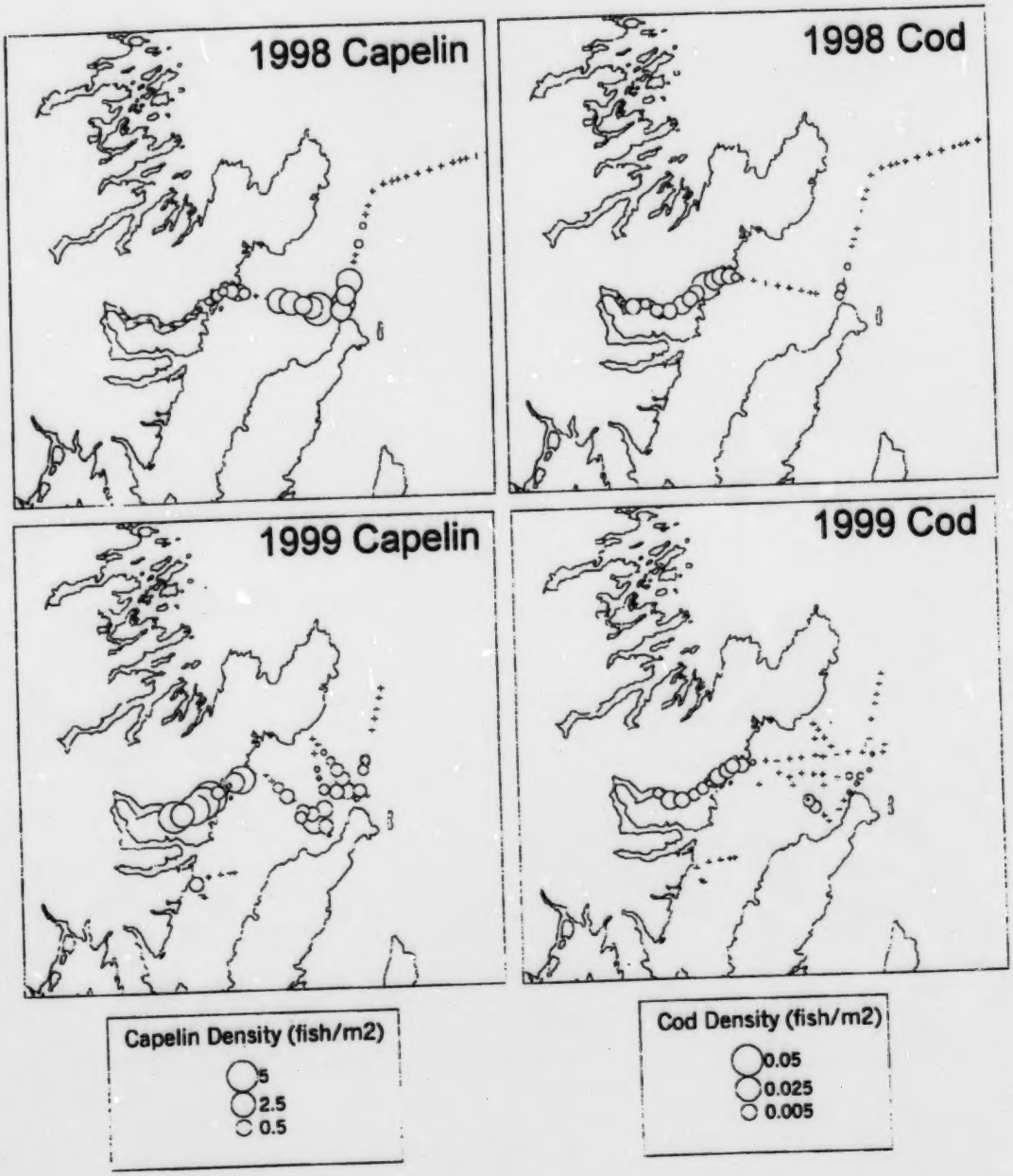

Fig. 5. Capelin and cod distributions in Trinity Bay from acoustic surveys in June 1998 and 1999. '+' symbol indicates no fish were detected.

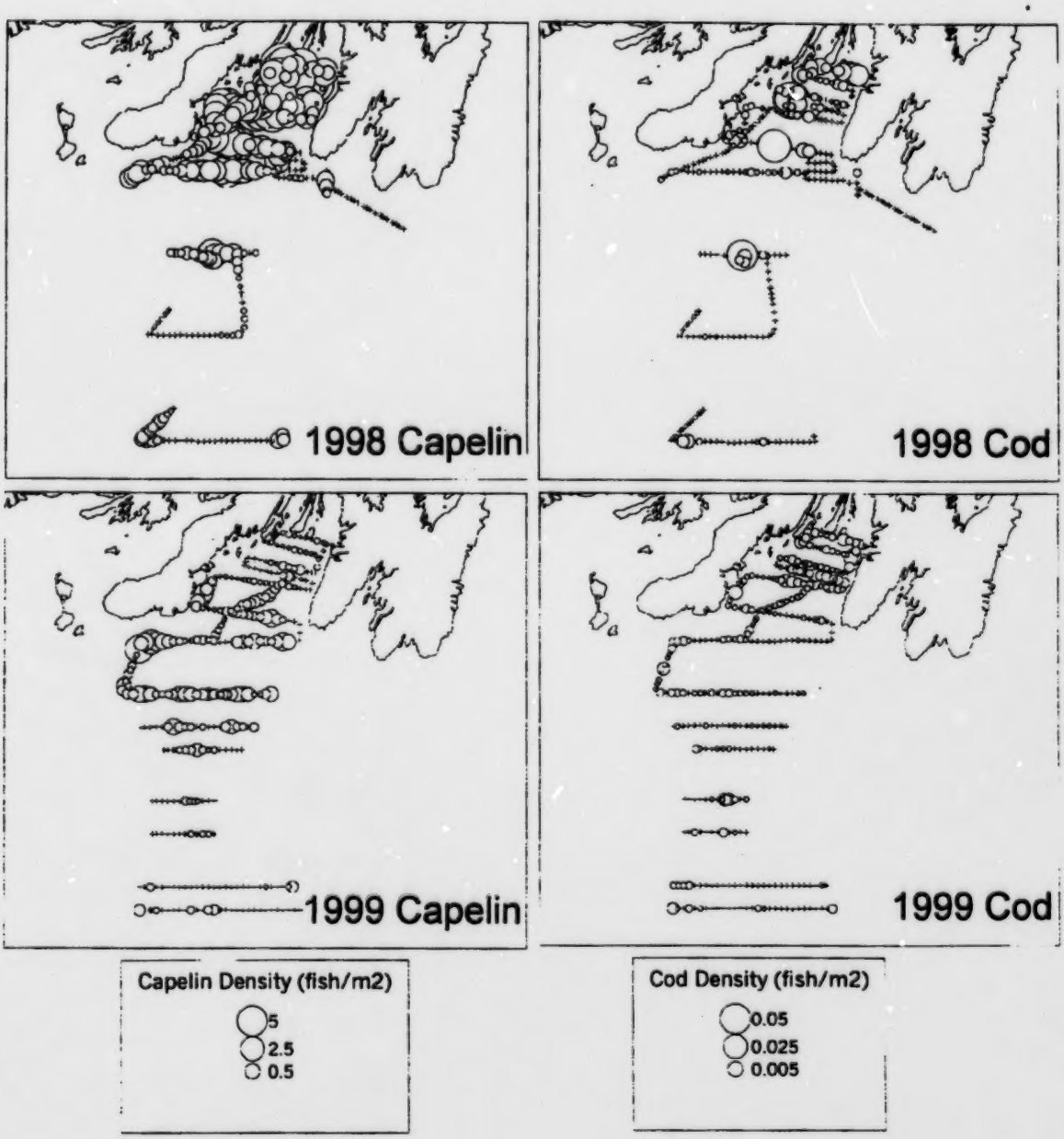

Fig. 6. Capelin and cod distributions in Placentia Bay and a portion of 3Ps from acoustic surveys in June 1998 and 1999. '+' symbol indicates no fish were detected.

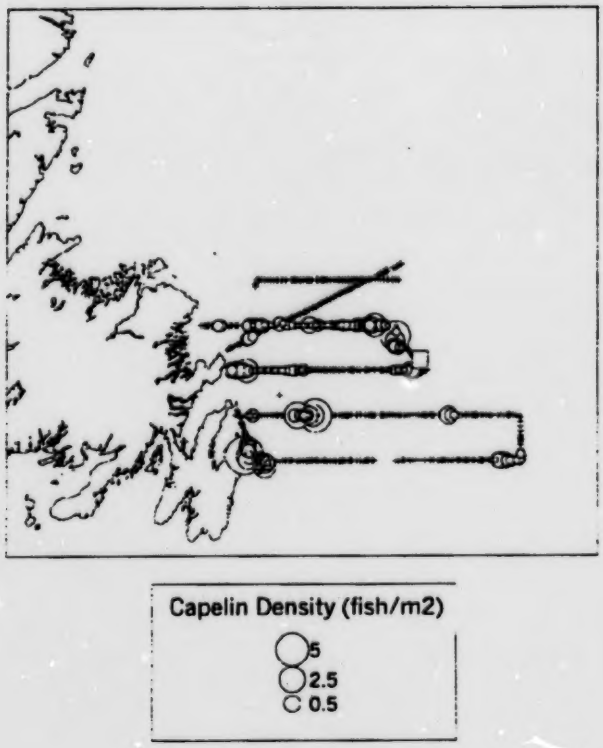

Fig. 7. Capelin distribution on the Northwest Newfoundland shelf from an acoustic survey in May 1999. '+' symbol indicates no capelin were detected. Small white square shows the only location where adult cod were observed.

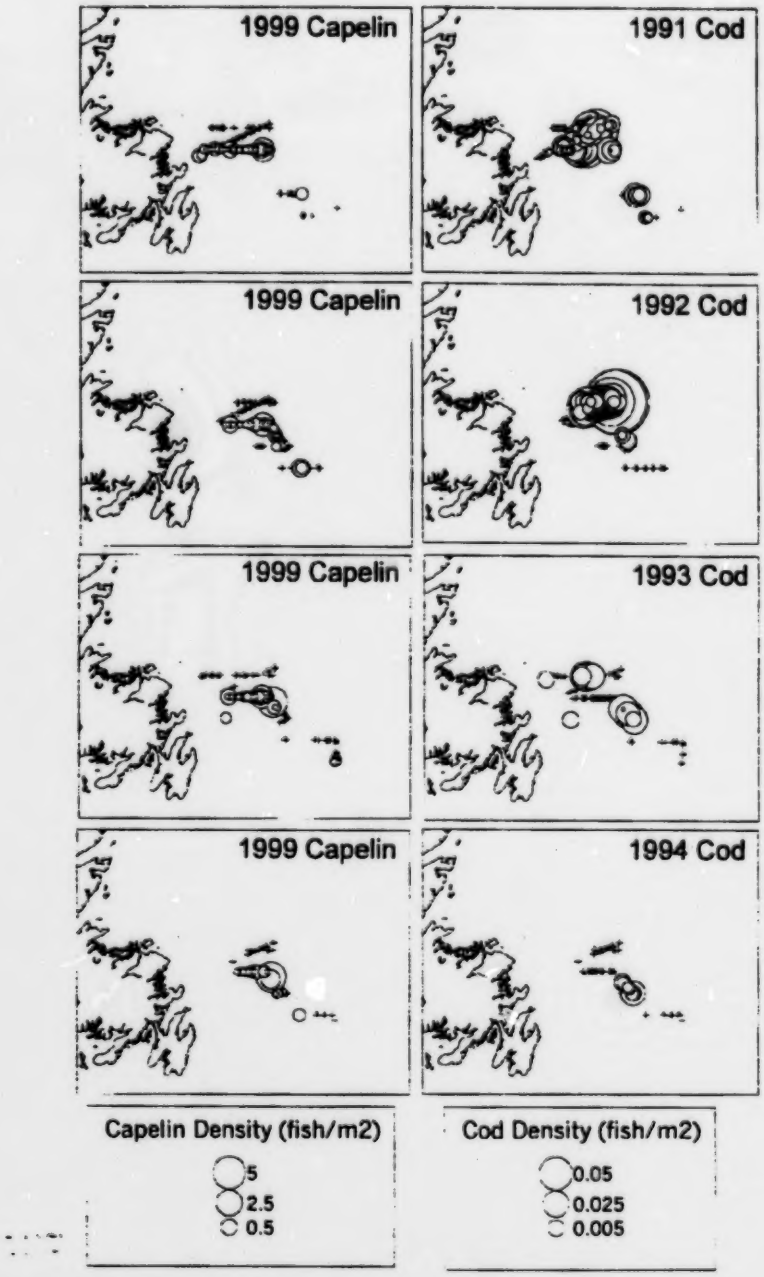

Fig. 8. Observed capelin and modelled cod distributions in the common area of the northeast Newfoundland Shelf surveyed in spring 1991-1994 and in 1999. Capelin distribution is from the spring 1999 survey. Modelled cod distributions show the acoustic densities that would have been observed in 1999 if cod were distributed offshore as in spring 1991-1994. '+' symbol indicates no fish were detected.

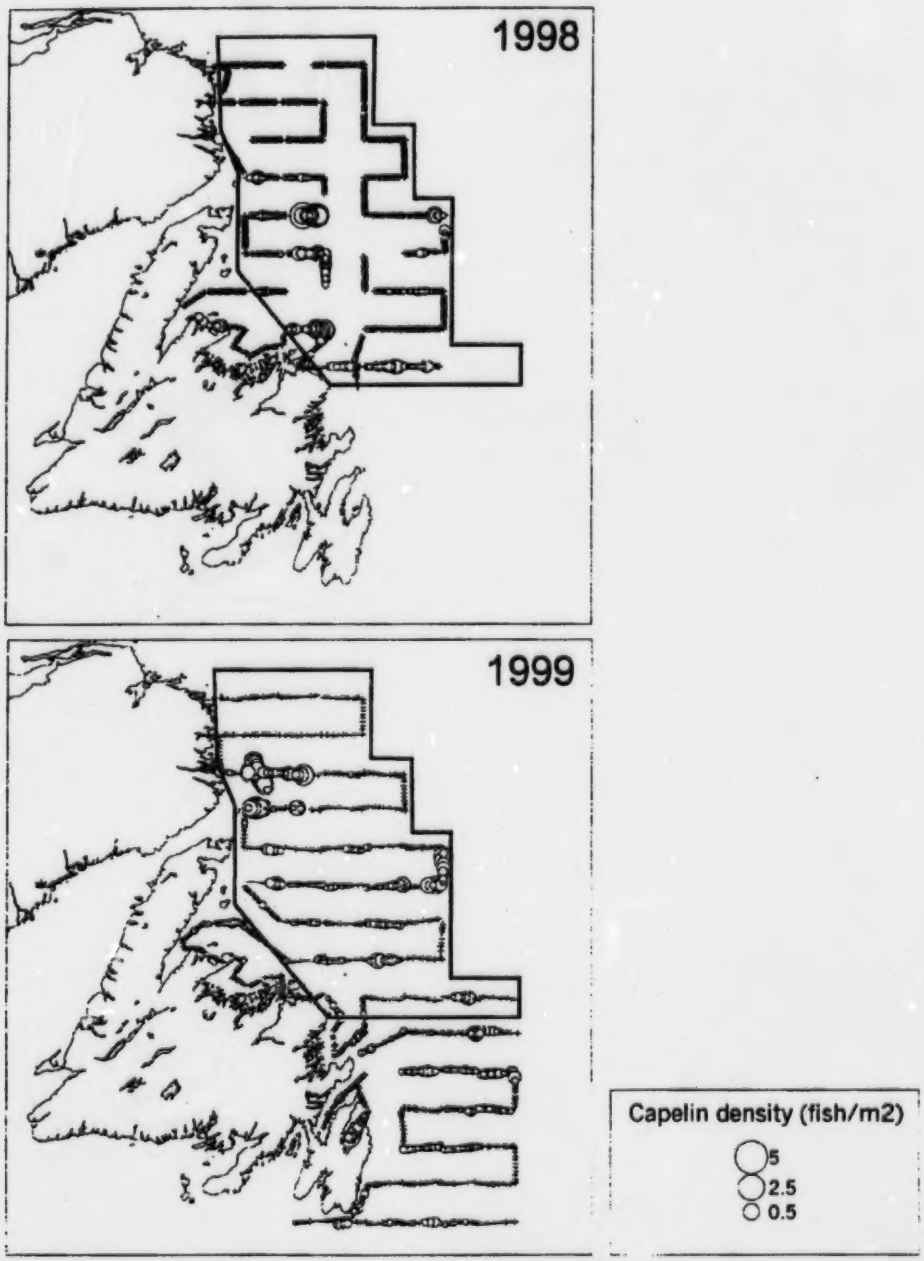

Fig. 9. Distribution of capelin during acoustic surveys in August-September of 1998 and 1999. '+' symbol indicates no capelin were detected. The part of the surveyed area in NAFO 2J3K used to estimate capelin biomass (Fig. 10) is boxed.

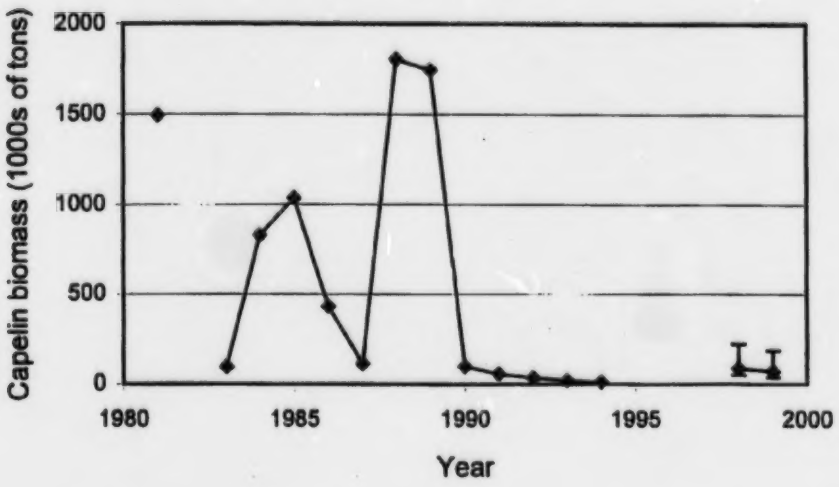

Fig. 10. Estimates of capelin biomass from Canadian fall (September-October) acoustic surveys in offshore NAFO 2J3K 1981,1983-1994. Data are from Miller (1995). Our estimates of capelin biomass from surveys in August-September 1998 and 1999 (see Fig. 9) are shown for comparison. A capelin target strength of –34dB kg^{-1} was used in all calculations. Error bars show 95% confidence intervals from bootstrapping uncertainty analysis.

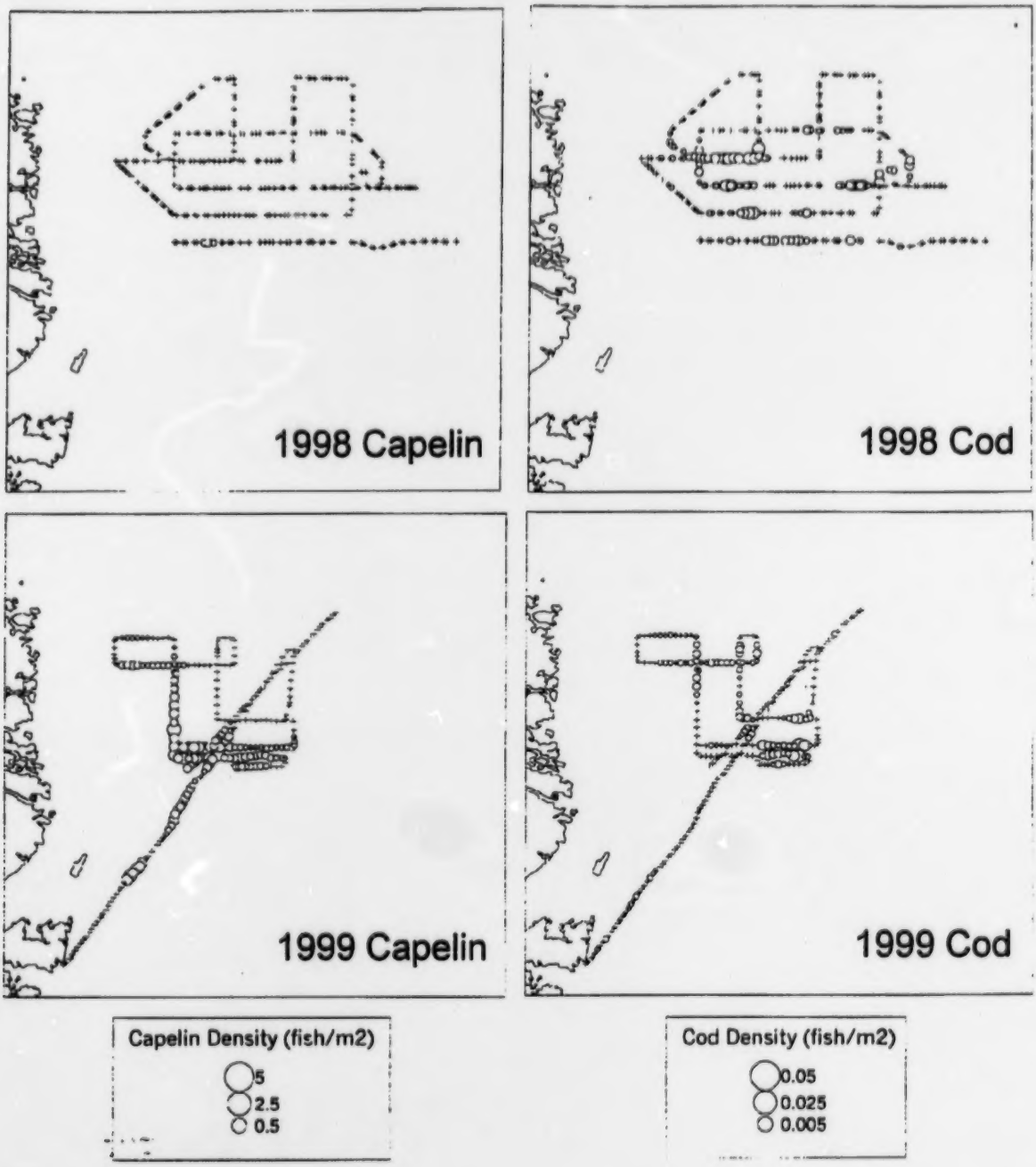

Fig. 11. Capelin and cod distributions in Hawke Channel, Labrador from acoustic surveys in June 1998 and 1999. '+' symbol indicates no fish were detected.

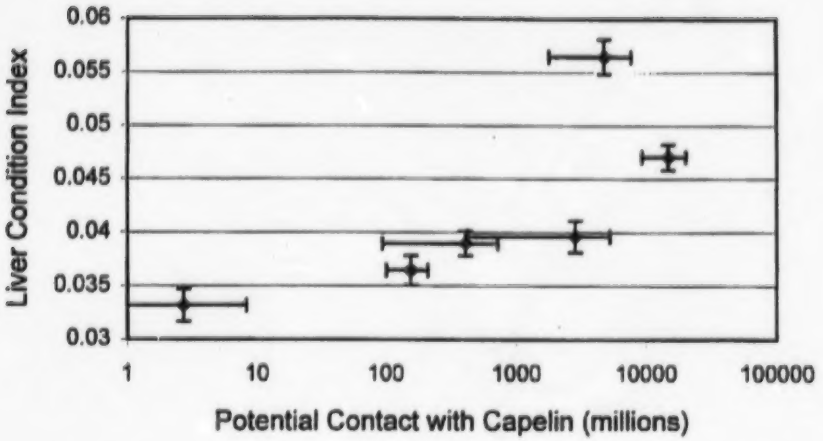

Fig. 12. Relationship between potential contact with capelin at a cod ambit radius of 40km and cod liver condition index (liver weight * gutted weight^{-1}). Plot shows means +/- 2 standard errors. Data are from spring acoustic surveys in Trinity Bay, Placentia Bay and Hawke Channel Labrador in 1998 and 1999. Estimates of liver condition were from cod 36-71cm only (c.f. Lilly 1994). Correlation is statistically significant (Spearman's rank correlation, $n = 6$, $rho = 0.943$, $p = 0.005$).